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Materials & Methods, 2 Figures, 1 Table & 2 appendices
In recent decades, many industrialized regions have been subject to enhanced atmospheric deposition of reactive nitrogen. This unintended fertilization is recognized to have stimulated forest growth, but nitrogen also strongly affects soil microbial activity and thus the recycling of carbon and nutrients in soils. Here, we present evidence from a meta-analysis that nitrogen deposition typically impedes carbon cycling through both rhizospheric and saprophytic pathways, except where the additional nitrogen remains insufficient to meet the nitrogen needs of trees and microbes. The associated, nitrogen-induced reductions in respiratory carbon losses are often of the same order of magnitude as the stimulation of wood production. These large reductions have a substantial effect on the net exchange of carbon with the atmosphere. Whether nitrogen deposition also affects soil carbon cycling in nitrogen-saturated and tropical forests remains an open question.

1. Introduction

Atmospheric deposition of reactive nitrogen (N), originating mainly from fossil fuel burning and artificial fertilizer applications, has increased three- to five-fold over the last century. In many areas of the globe, N deposition is expected to increase further, with global deposition rates projected to increase by a factor of 2.5 by the end of the century. Atmospheric deposition of N has many negative ecological effects in terrestrial and aquatic ecosystems, such as eutrophication and loss of biodiversity. Excessive N deposition can also result in soil acidification, loss of base cations and nitrate leaching into groundwater. However, low levels of atmospheric N deposition can have one positive effect: it stimulates...
plant growth and the associated uptake of carbon (C) from the atmosphere contributes to climate change mitigation. In 2007, Magnani and co-workers even revealed N deposition as the dominant driver of forest ecosystem carbon sequestration.

The publication by Magnani and colleagues generated an intense debate on the magnitude and sustainability of the N-induced C sink and its underlying mechanisms. Two responses contribute to the enhanced C sink strength of forests under elevated atmospheric N deposition: increased wood formation and accumulation of surface litter and soil organic matter (SOM). Accumulation of SOM could originate from increased soil C inputs, but this is not commonly observed in forests exposed to N deposition. In contrast, decreased rates of plant litter and SOM decomposition by enhanced soil N inputs have frequently been reported. Through a meta-analysis of measurements in N-addition experiments (Appendix S1) and a comparison of study sites exposed to elevated or background atmospheric N deposition (Appendix S2), we show that the negative effect of N on below-ground C fluxes is widespread, albeit not universal, in forest ecosystems. Despite the long history of evidence that N deposition slows decomposition, this effect has not been included in current C cycle models.
2. Empirical evidence for a reduction of soil C cycling by N

2.1. Litter quality modulates N effect on litter decomposition

It is well established that leaf litter with higher N (or high N to lignin ratios) decomposes faster than its lower N counterpart \(^{25-27}\), although this difference may revert during later stages of the decomposition process \(^{28}\). However, adding N to low N litter does not accelerate its decomposition. In an early review of more than 60 experiments on the effect of N application on decomposition of various types of organic matter, Kåre Fog \(^{23}\) concluded that “\textit{when all these papers are considered together, it is evident that no effect, or even a negative effect, of the addition of N to decomposing organic material is a very widespread phenomenon}”. Literature reviews have indicated distinct decomposition responses to N addition in litter with low versus high lignin content \(^{23,29}\). In agreement with earlier studies on leaf litter decomposition, N addition accelerates decomposition of low lignin litter. In contrast to the response of low-lignin litter, Fog \(^{23}\) concluded that: “\textit{in recalcitrant substrates the situation is completely different. Here negative effects of the addition of N are much commoner, especially if the lignin content is high, in direct contrast to the case above. Thus, the higher the lignin content, the smaller the amount of N tolerated}”. Almost exactly the same results were obtained in a recent comprehensive review with quantitative meta-analysis on the effects of N addition on litter decomposition \(^{29}\). Moreover, the overall mean response to N addition tended to be positive in short-term studies, but a significant decrease in decomposition rate (17\%) was detected in studies lasting longer than two years. Given that forest litter contains a substantial fraction of low quality litter (litter with high lignin and low N contents that decomposes very slowly) and the clear evidence that low quality litter is negatively affected by N addition, it is to be expected that atmospheric N
deposition would typically reduce litter decomposition in forest ecosystems. Our statistical meta-analysis applied to data from 20 N-manipulation experiments in forests suggested only a small and statistically insignificant decline in leaf litter decomposition rate (Fig. 1). However, in agreement with the previous studies, we found that N addition tends to accelerate decomposition in genera producing easily degradable leaf litter (e.g. *Acer, Populus, Betula*), whereas it clearly reduced decomposition rates in species with more recalcitrant litter (*Pinus, Picea, Fagus, Quercus*; Fig. S1). Moreover, all forests produce large quantities of lower quality litter, such as twigs, branches, and seed pods, which may be even more strongly affected by added N, but data are not available to test this hypothesis.

### 2.2. Heterotrophic respiration is commonly reduced

Respiration in aerobic soil involves the breakdown of organic molecules with, in aerobic soil, CO₂ as the main end-product. Release of CO₂ is therefore commonly used as a proxy for respiratory activity. Here, we define respiration by organisms obtaining their energy from the decomposition of litter and SOM as heterotrophic respiration. Heterotrophic respiration is thus an integrator of decomposition of organic matter in all stages of decomposition and in all soil layers, making its response to N addition more relevant to soil C cycling than that of leaf litter decomposition alone.

To mitigate variation due to methodological differences, we focus this review on heterotrophic respiration estimates obtained either from lab incubation or with the trenching technique, both of which physically separate the soil from the root inputs. Our statistical meta-analysis revealed that the average response of heterotrophic respiration to N addition is much more pronounced than that of leaf-litter decomposition alone. Averaged over 36 N-
manipulation studies in forest ecosystems, heterotrophic respiration declined by 15% when N was added (Fig. 1). Variation among experiments was very high, with responses ranging between a reduction of 57% and stimulation by 63% (Fig. 2, left panel). Forests exposed to elevated atmospheric N deposition are also observed to have lower heterotrophic respiration than forests receiving background N deposition (wet deposition < 5.5 kg N ha\(^{-1}\) a\(^{-1}\); Fig. 3). For forests with an NPP around 600 g C m\(^{-2}\) a\(^{-1}\), the reduction amounts to roughly 100 g C m\(^{-2}\) a\(^{-1}\) (Fig. 3). The different slopes of the two regressions in Figure 3 further suggest that at highly productive sites, where N is unlikely to be the most limiting nutrient, N deposition has a stronger negative effect than at less productive sites, where N immobilization is likely higher and the negative effect on heterotrophic respiration is only marginal.

It can be concluded that both episodic addition of high fertilizer amounts and chronic deposition of small amounts of N induce a decline in heterotrophic respiration in most—but not all—forest ecosystems.

2.3. Soil CO2 efflux response depends on productivity response

Soil CO2 efflux (SCE) is an important indicator for belowground C cycling \(^{33}\). Although heterotrophic respiration constitutes a substantial part of SCE, two important C fluxes, related to the presence of roots in soils, differentiate SCE from heterotrophic respiration. First, a major component of SCE is autotrophic in nature (root-, mycorrhizal- and rhizosphere respiration), coupling temporal variation in SCE to that in belowground C allocation and, ultimately, photosynthesis \(^{34-36}\). Second, rhizodeposition, the transfer of root-derived C compounds to soil, can stimulate microbial activity and thus prime decomposition of SOM \(^{37-39}\). This priming mechanism alters heterotrophic respiration, but could not have made a
contribution to the heterotrophic respiration measurements presented in section 2.2, which were all made in the absence of live roots.

As with heterotrophic respiration, there is convincing evidence that SCE declines following N addition, either through fertilization (-10%; Fig. 1) or through atmospheric N deposition (Fig. 4). In most studies, this negative effect appears almost instantaneously, while the negative responses persist for years after the addition of nitrogen has ceased \(^{24,40,41}\). Although the average response of SCE in fertilization experiments was clearly negative, SCE was found to be positively affected by N addition in roughly 25% of the 57 manipulation studies (Fig. 2, right hand panel). A closer look at the experiments where SCE increased following N fertilization revealed that these were mainly studies where N addition has the potential to strongly enhance photosynthesis: very young plantations (<4 years), where N addition may have accelerated canopy development, and CO\(_2\)-fumigated forest stands, where extra N helps to sustain the stimulatory CO\(_2\) effect on photosynthesis (Figures 2 and S2; \(^{42-44}\)). Part of the increased C availability was probably allocated belowground, stimulating rhizosphere respiration and microbial activity. We thus hypothesize that the increases in SCE observed in a sub-set of studies (Fig. 2, right hand panel) are attributable to enhanced photosynthesis following N enrichment.

Excluding the very young and CO\(_2\)-fumigated sites, the average decline in SCE amounted to –17% (Fig S2), roughly 150-200 g C m\(^{-2}\) a\(^{-1}\). Sites receiving more than 50 kg N ha\(^{-1}\) a\(^{-1}\) exhibited a stronger decline in SCE (-21%) than sites receiving doses of less than 50 kg N ha\(^{-1}\) a\(^{-1}\) which better mimics the effects of atmospheric N-deposition. Nevertheless, the response of SCE in this latter group remained significantly negative (-10%). Per unit N added, this reduction in SCE amounts to 36 g C per g N added. At a small number of sites older than 5 years and not enriched with CO\(_2\), SCE responded positively (or did not respond) to N
addition. At these few sites, we speculate that N might be limiting microbial growth and thus heterotrophic respiration (see section on heterotrophic respiration above).

2.4. Soil C increases, microbial biomass decreases

The response of plant-litter inputs (leaf-litter fall and fine-root production) to N addition is variable; both increases and decreases are frequently observed, and on average litter inputs are not affected (Fig. 1). In N fertilization experiments, the combination of reduced heterotrophic C losses and unaltered plant-litter inputs results in substantial soil C accumulation (relative increase of 10%; Fig. 1), corresponding to 19 g C per g N added. Thus, on average, about half of the reduction in SCE in the manipulation experiments may be due to C accumulating in the soil. This substantial increase in soil C should be interpreted with caution, because most studies report C pool changes only for the uppermost soil layers.

In a comprehensive review of results from $^{15}$N field experiments, long-term low dose N fertilizer experiments and ecosystem models, de Vries and co-workers also reported that N deposition substantially stimulated soil C sequestration. Taking all evidence into account, soil C sequestration in European forests in response to N deposition was estimated to range from 5 to 23 g C g N$^{-1}$, agreeing well with our estimate. Sequestration rates of similar magnitudes were also reported in other, more limited multi-site analyses.

The efficiency of soil C storage per unit N deposited declines with the amount of N added or deposited to the forest. This trend is expected, because as N availability increases, a larger fraction of it will be lost to groundwater and atmosphere, and the probability for adverse effects of N saturation increases proportionally.
Caution is, however, warranted when interpreting spatial correlations between N deposition and soil C sequestration across forests (Peter Högberg, personal communication). Within Europe, for example, N-deposition co-varies with natural soil nutrient availability. Human population centres have developed in the more fertile regions with good climate for N mineralization (not too dry, not too cold) and N deposition increased with population. Hence, soil C accumulation may be partly attributable to the more favourable, natural nutrient availability.

In agreement with the declining heterotrophic respiration and SCE, we observe a statistically significant decline (-11%) in microbial biomass (Fig. 1). A review on the effects of N deposition on microbial biomass showed that the average decline exceeded 20% in both temperate and boreal forests. When excluding very young forests and elevated CO$_2$ treatments from our analysis, we observe an average reduction of microbial biomass of 16% (Fig. S1), in line with the review by Treseder and with the response of SCE.
3. Processes underlying the reduction of soil respiration

Empirical evidence thus tells us that various aspects of belowground C cycling are negatively affected by N addition, that these effects are widespread, but that there are also conditions under which N addition accelerates decomposition and soil respiration (severe N-limitation, young forests, elevated CO2 experiments). The following mechanisms have been put forward in the literature to explain these observations (Box 1).

3.1 Reduced belowground C allocation

Nitrogen is the most important macro nutrient. With the exception of regions where other nutrients are more limiting, a large increase in N availability to trees reduces the need for investment of C in their nutrient-absorbing system. This induces a shift in C allocation in favour of production of aboveground tissues at the expense of the root system. In absolute values our data do not show clear differences in fine root NPP between N-fertilized and control plots (Fig. 1). However, the nutrient acquisition system is not limited to the root system and there is abundant evidence that N enrichment spectacularly affects the activity of the rhizosphere, and of mycorrhizal root symbionts in particular. In a N-supply gradient study, C allocation to fungal symbionts was the process that responded most to N addition. Drastic declines in the production of fruiting bodies by mycorrizal fungi, in the contribution of mycorrhizae to total microbial biomass, in mycorrhizal diversity (see Treseder for review), in mycorrhizal infection rates and survival, and in arbuscular mycorrhizal biomass, hyphal length and storage structures have all been reported in response to N addition. These results reflect reduced reliance of trees on fungal symbionts under high N deposition, which underlies the strong reduction in belowground C allocation.
The mere reduction in belowground C allocation has been shown to produce a direct negative effect on rhizosphere respiration and thus SCE. The reduction of C inputs into the soil is an important mechanism via which also decomposition and soil respiration may be altered (Box 1).

Mycorrhizal root symbionts have the capacity to degrade organic matter and their decline would therefore be expected to directly reduce decomposition. Additionally, mechanisms exist that are potentially even more relevant for the response of decomposition to the shift in belowground C allocation. Fine roots and especially mycorrhizal hyphae exude substantial amounts of soluble organic compounds and these compounds serve as C and energy sources for saprotrophic organisms that subsequently decompose organic matter in search of nutrients. This mechanism, known as the priming effect, is widely accepted to exert a major control over soil organic matter decomposition. By supplying less substrate to the decomposers, the N-induced reduction of belowground C allocation can thus be expected to impede decomposition of SOC.

The reduction in belowground C allocation thus contributes to the reduction in SCE (on average 36 g C per g N; section 2.3), but cannot explain the substantial increase in soil C (on average, 19 g C per g N; section 2.4). Such large soil C accumulation can only be explained by other mechanisms directly reducing the activity of saprotrophs.

3.2 Shifts in saprotrophic community structure or function

There are multiple mechanisms through which alteration of microbial community structure or function may affect decomposition of soil organic matter. First, addition of N could make
saprotrophic organisms switch from decomposing N-containing recalcitrant SOM to energy-rich rhizodeposits (preferential substrate theory \(^{63,65-67}\)). Alternatively, less efficient microbial populations (less C assimilated in biomass and more CO\(_2\) released per gram litter decomposed) that require little N could be outcompeted by populations that are currently nitrogen limited, but are more efficient \(^{41}\). Ågren and co-workers \(^{41}\) postulated that such a microbial community shift towards more efficient, N-demanding species could explain the observed reductions in SCE. Their model would also be consistent with the observed increases in soil C stocks and reduced microbial biomass if the new microbial populations also produced more recalcitrant organic molecules.

In the early 1960’s Mangenot & Reymond \(^{68}\) had observed that by adding N to sawdust, several species of wood-decomposing basidiomycetes lose their competitive ability, with different species dropping out at sequentially higher N levels. There is ample recent evidence that N addition to forest soils induces such shifts in microbial community composition \(^{47,69-71}\).

Whatever the exact mechanism explaining the reduced decomposition of recalcitrant SOC or of litter in final stages, alterations in the activity or expression of enzymes involved in the decomposition process are likely to play a key role. Cellulose decomposing – and phosphate acquiring enzymes were reported to increase following N fertilization, especially in N-limited ecosystems \(^{72-74}\), often accelerating cellulose decomposition \(^{74,75}\). In contrast, lignin-degrading enzymes, such as phenol oxidases and peroxidases are frequently down-regulated \(^{23,70,74,76,77}\), but see \(^{73}\). Several white-rot fungi were found not to synthesize their lignin-degrading enzymes in the presence of low molecular weight N compounds \(^{24,78,79}\), but this response varies among species \(^{23,80}\). One potential reason for this reduced synthesis of lignin-degrading enzymes is that lignolitic fungi have low efficiency and growth rate, and are therefore likely to be out-competed by other microbes, resulting in reduced ligninase activity and, hence,
lignin degradation\textsuperscript{41,68,81}. Many easily decomposable substrates are embedded in the lignin matrix within fresh plant litter\textsuperscript{23}. Thus, by degrading lignin more slowly, decomposition of all compounds within the lignin matrix is reduced\textsuperscript{76}.

These shifts in the expression and/or activity of various enzymes are thus likely to explain the observation that more labile litter types or compounds (such as cellulose) decompose faster following N addition, especially in the short term\textsuperscript{23,29}. In the long-term, the reduced production or activity of specific enzymes involved in the degradation of more recalcitrant compounds may be responsible for the negative effect of N addition. Although the concepts of altered microbial community structure and enzymatic spectra are appealing, Keeler et al\textsuperscript{73} were not able to find any correspondence between the N-addition effects on decomposition rates and on the activities of six key-enzymes involved in decomposition. Moreover, despite the strong evidence that lignin degrading enzymes are suppressed by N addition, this mechanism may only be valid in organic surface layers; in mineral soils neither lignin nor lignin-derivatives accumulate in soils exposed to N addition (e.g.\textsuperscript{71}). It is thus obvious that the molecular transformations in soils and the role of exo-enzymes in the degradation of the produced recalcitrant compounds are far from elucidated.

\subsection*{3.3 The role of stabilization mechanisms}

A major fraction of SOM is chemically or physically protected from microbial decay\textsuperscript{82}. If N addition were to interact with these stabilization mechanisms, a major effect on decomposition and heterotrophic respiration could be expected. One hypothesis often brought forward to explain the reductions in decomposition or heterotrophic respiration is abiotic stabilization of SOM\textsuperscript{23,24}. There is evidence of direct chemical incorporation of added
nitrogen into organic matter, producing heterocyclic forms of N (indoles and pyroles) or phenolic compounds polymerized by N-bridges, two groups of compounds that are highly resistant to degradation by microbial enzymes. By chemically protecting part of the organic matter available for decomposition, these abiotic reactions could thus reduce decomposition and enhance C sequestration (see also). However, $^{15}$N NMR spectrometry indicates that most of the retained N is in the amide form, indicating dominance of biotically mediated formation of recalcitrant SOM, possibly in response to an N-induced shift in microbial community composition. Although this downplays the role of abiotic reactions postulated to play an important role, it does not rule them out.

Incorporation of SOM within soil aggregates could also constitute an important physical stabilization mechanism. Aggregate formation correlates positively with rhizodeposition and microbial biomass and -activity, which all decline in response to N deposition. Hence, aggregate formation is not expected to explain the reduced SOM cycling.

Finally, soil acidification is also a stabilization mechanism through which decomposition of plant litter and SOM could be reduced. Given that soil pH is crucial to enzyme functioning, acidification could have a detrimental effect on microbial activity and thus on decomposition of SOM. Especially after chronic N deposition, poorly buffered soils where nitrification occurs will tend to exhibit lower pH. Nonetheless, even where soil acidification does not occur, negative effects of N addition are frequently observed. Hence, acidification may aggravate the response, but not explain it completely.
4. Implications

Both the N-fertilization manipulation experiments and the comparison between forest ecosystems subjected to background versus elevated N deposition provide evidence for a decline in SCE and heterotrophic respiration of the same order of magnitude as net ecosystem productivity (the actual net CO₂ uptake or release by ecosystems) reported elsewhere. It is thus not surprising that Magnani and co-workers identified N deposition as a better determinant of forest net ecosystem productivity than climate or site productivity. Networks of ecosystem CO₂ flux measurements are commonly used to construct greenhouse gas balances or to extract information on the determinants of these fluxes. The fact that N deposition often reduces heterotrophic respiration and SCE by such vast amounts implies that syntheses of CO₂ flux networks have to take N deposition into account when analyzing effects of e.g. climate on C cycling.

Eventually, all forests receiving elevated N deposition for decades or longer, will run into N saturation, a state in which the forest N cycle is no longer closed. Although the exact effects remain unclear, a decrease in productivity could be anticipated through the loss of base cations and lower phosphorus availability. Long-term responses may thus differ from the overall response reported here.

To date, N deposition has been elevated mainly in regions with relatively young, nutrient-rich soils, where N is often limiting plant growth (Eastern US, Europe, China). It remains to be tested whether N deposition will affect C cycling (stimulate wood growth and retard SOM decomposition) similarly in tropical (but also other) regions with older, severely weathered soils, where N may not be the most limiting nutrient. If N enrichment were to slow down
decomposition, then nutrient immobilization in accumulating SOC could negatively affect tropical forest productivity. Because 70% of the global primary productivity is realized in the tropics, a shift in N-deposition towards these regions might alter the global C-balance differently to that which might be expected by extrapolating the responses in temperate regions. Current understanding of C-nutrient interactions in severely weathered soils or soils with shortages of other nutrients remains extremely limited and N-addition manipulation studies in these areas too rare to allow statistical meta-analysis.

The evidence for altered belowground C cycling presented here highlights the need to incorporate N cycling and N deposition into terrestrial C cycle models; not only the potential N effects on productivity and interactions with increasing atmospheric CO2 levels, but especially the negative effects on decomposition, belowground C allocation and the coupling of C and N cycling in ecosystems. To do this properly, more work is needed to fully understand the relative importance of the different mechanisms at play (Box 1), on the long-term responses to chronic N deposition, as well as on the responses in tropical areas. Given that the size of the N-induced inhibition of below-ground respiration is of the same order of magnitude as the forest C sink, a better understanding of N deposition effects should be a strong, future research priority.
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IAJ, WD and SL conceived the manuscript. SL, WD, JAS, II and BEL provided the data. WD and SL performed the analyses. All authors collaborated in the writing.
Figure Legends

Figure 1: Effect of experimental N-addition on various forest C pools and fluxes as calculated by meta-analysis. Positive values indicate that N addition increased the factor, negative values indicate a decrease. Error bars indicate the 95% confidence interval. Data are the weighted means for n data points (n is listed along the righthand axis). Parameters listed are C inputs: litterfall (LF) and fine-root production (FRP), C pools: total tree biomass (TB), microbial biomass (Cmic) and soil C content (soil C), and C losses: litter decomposition (LD), heterotrophic respiration (Rh), root respiration (Rr) and soil CO2 efflux (SCE). Exact numbers can be found in Table S1.

Figure 2: Relative effect of N addition on heterotrophic respiration (Rh, left panel) and soil CO2 efflux (SCE, right panel) in the manipulation experiments included in the statistical meta-analysis (circles) and their overall mean effect size (open red squares). Open black circles are forest stands more than four years old that received no additional CO2 and their mean is represented by the open black square. Grey symbols are forest stands more than four years old exposed to elevated atmospheric CO2 concentrations, solid black symbols are forests of four years old or younger, and solid red symbols are forest stands of four years old or younger that also received CO2 fumigation. Error bars indicate the 95% confidence interval. In these young and/or CO2 fumigated forests, N deposition favours SCE (positive response), whereas in forests older than 5 years, N deposition has a negative effect on SCE almost consistently. The effect of N addition on Rh, in contrast, is more consistently negative and does not differ between very young and/or CO2 fumigated and older forests. Site information, data and references to all studies included in this analysis are given in Appendix S1.
Figure 3: Observed annual heterotrophic respiration rates (Rh) as a function of annual biomass production (NPP) in forests exposed to elevated or background N deposition. Open black symbols and dotted black line ($Y = 212 + 0.32X$) represent forests with wet N deposition < 5.5 kg N ha$^{-1}$ a$^{-1}$ (the current average deposition rate in unaffected forests). Solid red symbols and solid red line ($Y = 217 + 0.16X$) reflect forests with N deposition > 5.5 kg N ha$^{-1}$ a$^{-1}$ (affected by N deposition). The shaded areas surrounding the regression lines represent the 67% confidence intervals (1 SD). The data support the hypothesis that intercepts are equal ($p = 0.475$) but reject the hypothesis that slopes are equal ($p = 0.965$).

Figure 4: Observed annual soil CO$_2$ efflux (SCE) as a function of annual biomass production (NPP) in forests exposed to elevated or background N deposition. Open black symbols and dotted black line ($Y = 153 + 1.47X$) represent forests with wet N deposition < 5.5 kg N ha$^{-1}$ a$^{-1}$ (the current average deposition rate in unaffected forests). Solid red symbols and solid red line ($Y = 483 + 0.32X$) reflect forests with N deposition > 5.5 kg N ha$^{-1}$ a$^{-1}$ (affected by N deposition). The shaded areas surrounding the regression lines represent the 67% confidence intervals (1 SD).
Box 1

Insert figure around here ...

Box 1: conceptual scheme depicting the mechanisms that explain the N-induced response of below-ground C cycling and its variation (see also main text). The effects of N deposition on the saprotrophic system may be related to two, mutually non-exclusive mechanisms: (1) enhanced chemical stabilization of organic matter into compounds recalcitrant to microbial decay (magenta arrows) and (2) shifts in microbial enzyme synthesis and activity towards preferential decomposition of labile, energy-rich compounds, coupled with reduced decomposition of recalcitrant substrates (brown arrows). In the presence of roots, N-effects via altered rhizosphere C inputs (green arrows) influence rhizosphere respiration, but also C cycling through the saprotrophic system. Under increasing N availability, wood production is typically promoted at the expense of belowground C allocation, reflecting the reduced need for an elaborate nutrient acquisition system. Declining availability of energy-rich compounds, combined with excess nitrogen affects the functioning of the microbial community, producing a different enzyme spectrum. The reduced C available for mineralization results in further reduced saprotrophic biomass, and the associated increase in net N mineralization thus aggravates the above-mentioned, direct negative N effects on decomposition of recalcitrant soil organic matter.

Although retarded belowground C cycling in response to N addition is the general rule in forests, there are exceptions where soil respiration is enhanced by N enrichment. In severely N-limited forests, such as in the northern boreal zone, microbial biomass may grow following N addition, resulting in enhanced enzyme production and increased soil respiration. More commonly, however, N deposition may stimulate canopy photosynthesis. In N-limited, open
forests, as well as in very young, accruing plantations, N deposition can accelerate canopy closure and thus enhance light interception and photosynthesis. In N-limited systems (e.g. boreal forests or CO₂-enriched trees), leaf-level photosynthesis may also be enhanced by N addition. This increase in photosynthesis may offset the relative decline in belowground C allocation, such that more labile C enters the soil, fueling not only rhizosphere microbes but also saprotrophic microbes and their decomposition of recalcitrant SOC. Hence, although negative responses to N deposition and addition clearly dominate the literature, positive responses do occur.

The scheme presented in this Box 1 is, however, not valid for N-saturated systems where adverse effects such as acidification, cation leaching and altered vegetation composition may induce very different responses.